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The importance of phenotypic plasticity and local adaptation in driving intraspecific variability in thermal niches of marine macrophytes

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ABSTRACT

Climate change is driving the redistribution of species at a global scale and documenting and predicting species' responses to warming is a principal focus of contemporary ecology. When interpreting and predicting their responses to warming, species are generally treated as single homogenous physiological units. However, local adaptation and phenotypic plasticity can result in intraspecific differences in thermal niche. Therefore, population loss may also not only occur from trailing edges. In species with low dispersal capacity this will have profound impacts for the species as a whole, as local population loss will not be offset by immigration of warm tolerant individuals. Recent evidence from terrestrial forests has shown that incorporation of intraspecific variation in thermal niche is vital to accurately predicting species responses to warming. However, marine macrophytes (i.e. seagrasses and seaweeds) that form some of the world's most productive and diverse ecosystems have not been examined in the same context. We conducted a literature review to determine how common intraspecific variation in thermal physiology is in marine macrophytes. We find that 90% of studies identified (n = 42) found clear differences in thermal niche between geographically separated populations. Therefore, non-trailing edge populations may also be vulnerable to future warming trends and given their limited dispersal capacity, such population loss may not be offset by immigration. We also explore how Next Generation Sequencing (NGS) is allowing unprecedented mechanistic insight into plasticity and adaptation. We conclude that in the 'genomic era' it may be possible to link understanding of plasticity and adaptation at the genetic level through to changes in populations providing novel insights on the redistribution of populations under future climate change.

KEY WORDS: Local adaptation, phenotypic plasticity, population differentiation, macroalgae, seagrass, Next Generation Sequencing.

Introduction

Anthropogenic climate change has driven increases in both mean temperatures and the intensity and frequency of temperature extremes (heat waves) (Christidis *et al.,* 2005; Coumou and Rahmstorf, 2012; Lima and Wethey, 2012). Together, acute and chronic warming are resulting in the redistribution of species across the globe (Parmesan and Yohe, 2003; Burrows *et* al., 2012; Poloczanska *et al*., 2013), with major consequences for the structure and functioning of entire ecosystems (Walther *et al.,* 2002*;* Parmesan, 2006; Wernberg *et al*., 2016a; Pecl *et al*., 2017). Therefore, understanding when, where and how redistributions will occur has become a primary goal of contemporary macroecology.

When interpreting responses to warming, species are generally treated as single homogenous physiological units (Reed *et al*., 2011). This assumes populations have similar thermal tolerances irrespective of their latitudinal position and that any population can exist anywhere within its range. Therefore, range shifts at trailing edges are predicted to follow simple linear contractions from marginal populations persisting under warm distributional limits, as it is here where absolute temperature rises are most likely to fall outside of a species 'thermal niche' (Walher *et al.,* 2002; Parmesan & Yohe, 2003; Burrows *et al*., 2012; Sunday *et al.,* 2012, Poloczanska *et al.,* 2013). However, this approach fails to incorporate intraspecific differences in thermal niche from phenotypic plasticity and local adaptation (Box 1) as well as the dispersal capacity of a species. These factors are critical considerations as they can result in central populations also being vulnerable to warming trends (e.g. Atkins and Travis, 2010; Valladares *et al*., 2014).

Changes in thermal niche from both plasticity and adaptation can render central populations vulnerable to heatwaves as temperature rises may be too rapid for either acclimation or adaptation. When considering decadal-scale warming, adaptation will not be possible as contemporary warming out paces the rate of natural selection (Davis and Shaw, 2001; Jump and Penuelas, 2005; Quintero and Wiens, 2013). Therefore, range centre ecotypes may also experience temperatures that exceed their local thermal niche (Davis and Shaw, 2001; Etterson, 2004a,b; Jump and Penuelas, 2005). However, if differences are plastic, central populations will simply acclimate to range edge conditions (Sanford and Kelly, 2011). As such, disentangling the relative importance of these two mechanisms is crucial for understanding species' responses to warming. The dispersal capacity of a species is also a key consideration for assessing the vulnerability of central populations as it dictates which mechanism is favoured and

provides insight into the persistence of any population loss. For low dispersal species, local adaptation may be more prominent as natural selection is not homogenised by gene flow from populations under different selection pressures (Kirkpatrick and Barton, 1997). The unprecedented rate of contemporary climate change may also mean that such species are unable to track suitable extant habitat (Molinos *et al*., 2017). Therefore, any central population loss may not be offset by immigration from warm tolerant populations (Figure 1) (Davis and Shaw, 2001; Harte *et al.,* 2004; Atkins and

Travis, 2010; Sanford and Kelly, 2011; Valladares *et al*., 2014; Bennett *et al*., 2015).

There are multiple strategies for understanding local adaptation and plasticity but they are largely separated into two disparate fields (Table 1). Researchers either focus on ecological pattern associated with phenotypes of 'wild populations' or the underlying molecular process using model organisms in laboratory settings. There is rarely a crossover between disciplines as model organisms generally lack ecological importance while wild populations have historically lacked the necessary genomic resources. The advent of Next Generation Sequencing (NGS) is changing this dichotomy. It is now possible to gain mechanistic insight in 'wild populations' even where there is limited genomic knowledge of the species (Van Straalen *et al*., 2012; Alvarez *et al*., 2015). Given the strong drive in contemporary macroecology to understand both ecological pattern and the underling processes (Beck *et al.*, 2012; Keith *et al.*, 2012) we argue that merging these two fields provides an exciting opportunity to understand how different thermal physiologies may affect species responses to warming.

In comparison to terrestrial systems, marine taxa have been underrepresented in attempts to understand the implications of thermal plasticity and adaptation. Marine macrophytes (seaweeds and seagrasses) in particular exhibit a number of traits to suggest that these mechanisms may be prevalent. Unlike many marine species that have large dispersal capacities, marine macrophytes generally exhibit restrictive dispersal with seaweed spores settling within a few metres of the parent alga (Dayton 1985, Schiel and Foster 1986, Santelices 1990; Kendrick and Walker, 1991; Norton 1992; Kendrick and Walker, 1995) and seagrass pollen and seed dispersal often limited to the meadow in which the adult plant inhabits (Zipperle *et al*., 2011, Kendrick *et al*., 2012). This often results in highly structured distributions (Valero *et* al., 2011; Assis *et* al., 2015; Nicastro *et* al., 2013; Robuchon *et al*., 2014; Neiva *et al*., 2015) and

means local ecotypes may be a common characteristic (e.g. Gerard and Dubois, 1987) in marine macrophytes, with any associated population decline unable to be ameliorated by migration (Bennett *et al*., 2015; Assis *et al.,* 2017; Molinos *et al*., 2017). However, it should be noted that even within this group some species exhibit larger scale dispersal capacities that can result in a closer tracking of habitat as niches shift (Duarte *et al*., 2013). Marine macrophytes are also underrepresented in molecular studies investigating mechanisms underlying thermal physiology. Historically they have been poor genomic models due to a lack of sequence data and difficulties with rearing species with complex life cycles in laboratory settings (Waahland *et al*., 2004; Pearson *et al*., 2010). However, the recent availability of reference genomes (red algae; Collen *et al*., 2014; brown algae; Ye *et al*., 2015; seagrass; Olsen *et al*., 2016) and the unprecedented mechanistic insights that can be gained using NGS provide the opportunity to signficiantly advance current understanding. In many ways marine macrophytes are ideally suited to understanding how temperature drives changes in phenotype. Unlike many terrestial taxa they have very narrow linear range distributions (length >1000's km; breadth < 0.5 km) and so gradients are not confounded by covarying factors. Moreover, gradients are often replicated across multiple coasts (e.g. kelps across both sides of the Atlantic).

Warming mediated range shifts have been observed for marine macrophytes across the world (Marba and Duarte, 2010; Wernberg *et al*., 2011; Smale and Wernberg, 2013; Wernberg et al.,2013; Thomson et al., 2015; Wernberg et al., 2016; Krumhansl et al.,2017) and are predicted to continue as warming progresses (e.g. Martinez *et al*., 2012; Jueterbock *et al*., 2013). Perhaps the most notable is a ~ 1,250 km range contraction of the intertidal fucoid, *Fucus vesiculosus,* from Morocco polewards to the mid Iberian Peninsula over a 30 year period (Nicastro *et al.*, 2013). Many marine macrophytes are foundation species that provide habitat and resources for other species and structure entire communities and ecosystems (Steneck *et al*., 2002; Teagle *et al*., 2017). Therefore, the ecological implications of macrophyte population losses are far-reaching. Where seaweeds and seagrasses form forests and meadows they rank amongst the world's most diverse and productive ecosystems (Duarte and Chiscano, 1999; Steneck *et al*., 2002; Smale *et al*., 2013) rivalling that of terrestrial rainforests (Mann, 1973). Moreover, coastal vegetated habitats are of considerable socioeconomic importance to human populations through the provision of ecosystem goods and services (e.g. commercial fisheries, nutrient cycling, direct harvesting, biogenic coastal defence) which can be worth billions of dollars annually (Beaumont *et al*., 2008; Bennett *et al*., 2016). Thus, gaining an understanding of whether central

populations may also be vulnerable to warming is of great ecological and socioeconomic concern.

We synthesized existing literature examining intraspecific differences in thermal physiology across large geographic scales in marine macrophytes to ascertain (a) the extent to which marine macrophytes exhibit intraspecific variability in thermal niche and (b) the relative importance of plasticity and adaptation in underpinning these patterns. We also examined the current state of molecular understanding of thermal plasticity and adaptation in marine macrophytes, and coastal marine ecosystems more generally, with particular emphasis on the use of NGS platforms in elucidating these mechanisms.

Literature Survey

Marine macrophytes comprise thousands of species with diverse evolutionary histories spanning four phyla; Rhodophyta (red algae), Chlorophyta (green algae), Ochrophyta (Phaeophyceae/brown algae) and marine angiosperms (seagrasses, mangroves and salt marsh plants). In the context of this review, we focussed on macroalgae (hereafter 'seaweeds') and seagrasses, which are 'fully marine' and predominantly influenced by sea water temperature, and excluded salt marsh and mangrove species which are primarily influenced by aerial temperatures.

We conducted a systematic review of the published literature using ISI Web of Science and Google Scholar. Search terms used were: Thermal ecotypes, local adaptation, phenotypic plasticity, thermal divergence, macrophytes, tolerance limits, thermal phenotype, niche partitioning, latitude, seagrass, kelp, fucoids, and seaweed. Combinations of search terms were used along with reference lists of identified articles. We limited the scope of our review to studies that explicitly measured a response to an experimental temperature treatment, specifically through common garden or transplant experiments from at least two populations occupying different thermal regimes. By doing this, intrinsic variation between sites was eliminated and the response being measured was directly attributable to measurable temperature differences. Consequently, our dataset did not include *in situ* field observations of differential performance, morphology, phenology or other life history traits (e.g. Araújo *et al*., 2011, 2014; Andrews *et al*., 2014). We also omit studies dealing with two cryptic species (Oppliger *et al*., 2012) or those that were confounded by other covarying environmental gradients. Therefore, studies from the Baltic Sea (e.g. Tatarenkov *et al*., 2005; Lago-Leston *et al*., 2010) were not included due to the confounding salinity gradient that can invoke other

distinct physiological ecotypes (Karsten, 2012). Where studies examined more than one species, all species that met the suitability criteria were included to ensure that the broadest range of species could be explored. For dependent variables we included whole organism responses such as growth and survival and also proxies including photosynthesis, respiration and gene expression. As seaweeds have a heteromorphic life cycle with a macroscopic sporophyte stage and microscopic gametophyte stage and plasticity and adaptation can affect both, we included both stages. In total we identified 42 studies that met the suitability criteria. The complete paper was then scrutinized to identify whether intraspecific variation between populations was observed and whether the underlying cause of variability was deemed to be plasticity or adaptation (based on the author's conclusions). We determined the spatial scale between tested populations by calculating minimum distance by sea in Google Earth.

General Patterns

From the 42 studies, 29 species spanning the four macrophyte groups (i.e. brown, red, green algae and seagrasses) were examined encompassing the majority of the worlds temperate systems (Figure 2). Intraspecific differences in thermal physiology were found in 90% of the identified studies. Brown macroalgae were overwhelmingly the most studied group (Figure 3a) (77% of total studies) with representative examples from the majority of the world's temperate systems (E and W Atlantic; E and W Pacific; Indian Ocean). African examples were lacking both from the West African region and South Africa. Other seaweed groups were far less represented, with only two studies focusing on green and one on red macroalgae. Six studies focussed on seagrass but were limited to European populations (but see Jueterbock *et al*., 2016 for Europe vs. N American comparison) rather than populations within regions of greatest diversity such as the Indo-Pacific (Green and Short, 2003), and studies focused solely on the genus *Zostera*.

The overwhelming number of studies investigated differences between only two study regions (Figure 3b). The geographic scale of investigated studies varied from 350 to 6000 km (Figure 3c). In seaweeds it was most frequently 500 – 1499 km while the isolated nature of investigated seagrass meadows (Mediterranean vs North Sea) meant that sites were over > 4500 km apart. A common garden approach was by far the most frequently employed experimental design while only five studies utilised a transplant approach (Figure 3d) of which one was reciprocal, two were warm-to-cool and two cool-to-warm. Performance was directly assessed measuring growth or survivability in 53% of studies with the remainder

using proxies such as photosynthesis, metabolic rate or gene expression (Figure 3e). In common garden studies, treatments were either applied in a chronic or acute fashion which was generally reflective of the vertical position of the study species/population, either in the intertidal or subtidal. Chronic studies varied in their duration but were generally in the order of days and weeks, which are considerably shorter than typical durations of experiments on terrestrial plants, which are in the order of months and years (Franks *et al*., 2014).

Across the studies there was a clear disparity between those investigating discrete warming events (i.e. marine heatwaves, for definition see Hobday et al., 2016) and those investigating gradual warming. Almost all seaweed studies (but see Bennett *et al.,* 2015) were concerned with gradual warming or characterising the relationship between temperature and growth, or in intertidal species, investigating the capacity to tolerate acute temperature shocks mimicking the harsh conditions experienced during low tide emersion (e.g. Gerard and Dubois, 1988; Pearson *et al.,* 2009). In contrast, seagrass studies almost solely dealt with the differential ability to tolerate discrete heatwave events (Figure 2f) (e.g. Gu *et al.,* 2012). It is unlikely that this disparity in focus between the two groups is a product of differential resilience to either type of warming *per se*, as heatwave events are known to affect seaweeds (Dayton, 1985; Smale and Wernberg, 2013; Wernberg *et al*., 2013) and gradual decadal scale warming also affects seagrasses (Marba and Duarte, 2010). It is more likely due to the more conspicuous impacts of summer heatwaves on seagrass populations, which often exceed physiological tipping points (Orth *et al*., 2006; Waycott *et al.,* 2009) and may interact with a range of climate and non-climate anthropogenic stressors. Seagrass-dominated habitats are critically threatened in many regions and in 'global crisis' (Orth *et al*., 2006), so understanding how different species and populations respond to heatwaves has attracted considerable research focus in recent years.

Temperature variability influences macrophytes across all stages of their life cycle (Novaczek., 1984; Matson and Edwards, 2007). Therefore, differentiation in thermal physiology in seaweeds can occur at the macro and microscopic stages. While the vast majority of studies in our dataset focused on adult sporophytes, six also examined differential thermal physiology of microscopic stages. These studies reported both pronounced variability and little-to-no variability between populations. For example, *Ecklonia radiata* populations in Australia and New Zealand were found to have optimal performances reflective of those experienced by the environment in which they persist (Novaczek, 1984; Mohring *et al*., 2007) whereas no intraspecific variability in the gametophyte stage was reported for four kelp species in the northeast Atlantic (Bolton and Luning., 1982). Whether

such differences will be important in the context of species redistributions will depend on the comparative vulnerability of the life stages. If, for example, the sporophyte stage is most sensitive to warming then intraspecific variation in the microscopic stage will likely be less important in driving changes at the population level. However, vulnerability assessments across life stages are still lacking for most species (Novaczek., 1984; Matson and Edwards, 2007).

Disentangling Plasticity from Adaptation

While the vast majority of studies observed clear differences in the thermal physiology, in most cases the underlying mechanism for such differences was assumed to be adaptation despite the experimental design (usually common garden with short acclimation times) often not allowing for definitive inferences to be made. In most cases the potential for intraspecific variation to be underpinned by plasticity was not considered. Transplants are seen as the most direct and effective method to determine adaptive variation (Kawecki and Ebert, 2004). When such approaches were employed variation in thermal phenotype was still observed. In range centre to range edge transplants (cool to warm conditions), which simulate warming scenarios, studies either found that central populations could not tolerate range edge conditions (e.g. Gerard and Dubois, 1987, Bennett *et al*., 2015) or performed poorer than local individuals (e.g. Saada *et al*., 2016).

Despite often imposing acclimation periods under common conditions in order to eliminate artefacts of the thermal history experienced by each population, it is still difficult to unequivocally conclude a genetic origin for any observed differences because plasticity can be permanent or passed on to subsequent generations (Herman and Sultan, 2011). Such 'transgenerational plasticity' can mimic or obscure patterns of adaptation (Santon and Galen, 1997; Agrawal, 1999). Even when common acclimation conditions are utilised over the entire life of an individual, transgenerational plasticity, from maternal effects or 'epigenetics', can be remarkably persistent (Zamer and Mangum, 1979; Schmitz and Ecker, 2012). This shortcoming can be overcome by rearing offspring from each population over several generations, under the same rearing conditions, and then perform transplant experiments or common garden experiments on $F_{2/3}$ offspring (e.g. Kuo and Sanford, 2009).

Two studies investigated differences in thermal tolerance on progeny of the target populations reared in common conditions which can conclusively disentangle plasticity from adaption. Gao *et al*. (2013) performed a warm to cool transplant between southern and

northern Japan on the commercially exploited kelp *Undaria pinnatifida* to determine if warm ecotypes could be used in farmed areas that have been affected by recent warming. The transplanted kelps were self-crossed with one another over three generations and common garden experiments were performed on the F_3 offspring. They found the warm-cool transplants maintained their respective thermal physiological characteristics both in terms of higher survival at higher temperatures and higher growth. Similarly, Bolton (1983), took advantage of *Ectocarpus siliculosus* cultures taken throughout its range and held in common culture conditions for a number of years and found that despite long term incubation, warmer populations maintained a greater thermal tolerance and optimal growth at higher temperatures.

Significance and Limitation of Findings

The high proportion of studies that reported marked differences in thermal physiology between populations suggests that this pattern is widespread in marine macrophytes. Such differences combined with low dispersal could indicate that central populations may be vulnerable to future warming trends. While most studies do not effectively disentangle the underlying mechanisms, it is plausible to assume that adaptation plays an influential role. The fine scale genetic structuring observed for many species (e.g Valero *et al*., 2011; Robuchon *et al*., 2014) suggests that adaptation may be favoured, while experimental evidence also indicates that developmental plasticity and carry over effects do not drive differences in thermal phenotype along environmental gradients in seaweeds (Hays, 2007). Thus, central populations may be vulnerable to both gradual and acute warming trends. Even if intraspecific variability is a consequence of plasticity, the susceptibility of range centre populations to extreme temperatures experienced during heatwaves is still a cause for concern. Indeed, recent studies have directly highlighted central population vulnerability in marine macrophytes. For example, Bennett *et al*., (2015) showed that range centre and trailing edge populations of the fucoid, *Scytothalia dorycarpa,* in Western Australia share a thermal safety margin of 2.5 °C. Locations where this threshold was exceeded during the Ningaloo Niño heatwave in 2011 (Feng *et* al., 2013) experienced widespread population loss and shifts in community structure (Smale and Wernberg, 2013). Similarly, Saada *et al*., (2016) concluded that intraspecific differences in thermal tolerances of the intertidal fucoid, *Fucus vesiculosus*, may render central populations along the Iberian Peninsula vulnerable to warming.

In terrestrial systems researchers are beginning to directly incorporate intraspecific variation in thermal niche in predicting future species distributions (e0.g. O'Neil *et al*., 2008; Wang *et al*., 2010; Valledres *et al*., 2014; Martinez *et al*., 2015). By serendipitously using historic provenance data (Matyas, 1996) these studies find that incorporation of such variation is vital to accurately predict habitat suitability, with both more pessimistic (O'Neil *et al*., 2008) and optimistic (Pearman *et al*., 2010; Oney *et al.,* 2013) predictions found. However, these efforts are currently restricted to terrestrial forests as outside of the large historic forestry provenance datasets the necessary information from transplants, provenances tests and common garden studies are lacking. In order for species response to warming to be more accurately predicted fine scale regional data are urgently needed.

Whilst central population vulnerability is still poorly understood there is increasing debate relating to the feasibility of potential mitigation strategies. 'Assisted migration', whereby preadapted individuals are introduced to vulnerable populations from warmer parts of a species distribution, is gaining traction (Aitken *et al.*, 2008). By introducing adaptive alleles to recipient populations, or simply increasing their frequency, it is anticipated that local thermal tolerances will be boosted preventing adaptive failure. Indeed, framework policies are already being developed in terrestrial forests (McLachlan *et al.*, 2007; Aitken & Whitlock, 2013; Williams & Dumroese, 2013). With regards to marine macrophytes, the concept of assisted migration is not new. Reforestation of seagrass meadows, which are experiencing widespread global habitat loss from a multitude of stressors (Orth *et al.*, 2006), has been attempted many times, although only ~37% of restorations have been successful (Katwijk *et al.*, 2016). Examples from seaweeds are distinctly lacking which may be due to the inherent logistical challenges associated with transplanting and maintaining seaweeds on rocky reefs, often in highly dynamic environments. However, recent reintroduction of the locally extinct fucoid, *Phyllospora comosa*, into the metropolitan waters of Sydney, Australia (Campbell *et al.*, 2014) show that while more difficult than simple reseeding in terrestrial forests, restoration of marine macrophytes may be feasible. Assisted migration may also be a commercial consideration for marine macrophytes. In East Asia kelps are intensively farmed, while in Europe they are predominantly exploited from wild populations, although small scale commercial European kelp aquaculture is becoming increasingly common. As temperatures rise and yields fall, identifying warm tolerant strains may also be an effective management solution. Indeed, Asian *Sacharina japonica* farms are currently developing this approach in light of recent warming-induced crop failures (Pang *et al.*, 2007; Liu & Pang, 2010; Gao *et al.* 2013).

Molecular Mechanisms for Plasticity and Adaptation

We identified a number of studies using gene expression to measure thermal tolerance. In seaweeds these studies investigated the differential upregulation of a handful of Heat Shock Proteins (Hsps) in response to common garden temperature stress. Studies reported clear differences in thermal set points in the expression profiles of Hsps depending on geographic location (Henkel *et al*., 2009; King *et al*., *in review*) which is indicative of local adaptation (Barua and Hackathon, 2004). For example, Henkel and Hofmann, (2008) observed greater temperatures of maximal expression and shutdown of *Hsp70* to common garden temperature stress in the kelp, *Egregia menziesii*, along the west coast of N America. However, outside of these relatively simplistic approaches based on Hsp gene expression, mechanistic studies are lacking. There have been efforts to understand the transcriptomic responses to low tide emersion stress but these studies have been from a single location and used non NGS approaches such as cDNA microarrays and expressed sequence tag (Table 1) (Collen *et al*., 2007; Pearson *et al*., 2010). To date, no studies have employed RNAseq, which allows for quantification of the entire transcriptome, to determine how gene expression modulates differences in thermal tolerance, either in single populations or across regions.

A more comprehensive understanding of how transcriptome-wide gene expression modulates thermal tolerance has been developed for seagrasses. Franssen *et al* (2011) subjected North Sea and Mediterranean populations of *Z. marina* to a similar heatwave scenario and measured transcriptomic response and recovery with RNAseq. They found gene expression profiles in response to heatwave stress were similar between populations, dominated by classic Hsps, but responses differed considerably during a recovery period. The transcriptomic response of warmer populations returned to control conditions almost immediately. Conversely, northern populations failed to recover and expressed genes involved in protein degradation, indicating that proteins were damaged irreversibly and needed to be removed from cells. Franssen *et al* (2011) coined the term ‘transcriptomic resilience’ to describe the ability to return gene expression to control levels. This pattern of transcriptomic resilience was subsequently reported for northern and southern populations of *Z. marina* along the US Eastern Seaboard (Jueterbock *et al*., 2016) and similar patterns can explain differential bleaching in coral (Seneca and Palumbi, 2015). As RNAseq becomes more commonly used in ecological genomics, transcriptomic resilience may emerge as an important driver of thermal divergence across other systems and taxa.

Marine macrophytes have received considerable attention from a phylogeographic and population genetic perspective where studies try to understand patterns of gene flow and the distribution of genetic diversity (e.g. Provan *et al*., 2005; Olsen *et al*., 2011; Coyer *et al*., 2011; Diekmann and Serrao, 2011; Maneiro *et al*., 2011; Assis *et al*., 2013; Provan *et al*., 2013; Neiva *et al*., 2016). There have also been efforts to understand how hybridisation can facilitate adaptation to challenging habitats (e.g. Coyer *et al*., 2006). However, these studies have utilised neutral markers in their approach and the functional basis for local adaptation have been rare. Despite coastal systems being earmarked as ideal candidates to "find the genes that matter in ecology" (Schmidt *et al*., 2008) our knowledge of the molecular processes underpinning thermal adaptation is distinctly lacking in marine macrophytes. We found no studies utilising NGS genome scans to identify candidate loci under selection in relation to temperature, or indeed any other environmental gradient. This is surprising as macrophytes are known to form a number of different environmental ecotypes (Eggert, 2012; Karsten, 2012) and searches for adaptive signatures have been conducted in both seagrass and seaweed research. For example, loci attributed to osmoregulation and desiccation have been identified as candidate genes under selection using pre NGS genome scans along depth and salinity gradients (Oetjen and Reusch, 2007; Coyer *et al*., 2011). Despite the potential for NGS genome scans to determine how adaptive variation is distributed throughout marine macrophyte ranges being previously voiced (Provan *et al*., 2013) the benefits in identifying signatures of selection that are afforded by such platforms are not being felt in general marine botanical research.

No studies were conducted on DNA methylation (Box 1) most likely due to research on the epigenome being in its real infancy. However, some insight was found in the sequencing of the brown algae, *Ectocarpus siliculosus* that revealed an absence of detectable levels of cytosine methylation in its genome (Cock *et al*., 2010). Therefore, transgenerational epigenetics mediated through DNA methylation may not be an important mechanism in this group, although this requires confirmation.

What can be learnt from other marine taxa?

In lieu of relevant examples in marine macrophytes we draw upon evidence from other coastal marine taxa and ecosystems to examine the mechanisms known to influence thermal physiology.

Insights into how gene expression mediates thermal tolerance are emerging from other marine systems, aside from seagrasses. 'Frontloading' of Hsps and proteins involved in apoptosis regulation, tumour suppression, immune response and cell adhesion has been found to raise intraspecific thermal tolerance in corals and intertidal gastropods (Barshis *et al*., 2013; Gleason and Burton, 2015). The acclimation capacity of the transcriptomic response can also change between populations. Transplanting corals from stable to variable habitats causes a reduction in performance as patterns of gene expression cannot match resident populations. Conversely, in variable to stable transplants no reduction in performance is observed as full transcriptomic acclimation is achieved (Palumbi *et al*., 2014; Kenkel and Matz, 2016). To date, transplants have been based on variable and stable rock pools and along coastal depth gradients. However, if future studies are conducted on range edge and range centre populations the molecular basis for regional scale differences in thermal tolerance limits may be revealed.

Recent genome scans have identified candidate genes under selection related to energy metabolism in red abalone, *Haliotis rufescens,* (Wit and Palumbi, 2013) and the bivalve, *Macoma balthica* (Pante *et al*., 2013), and heat shock proteins in the red band trout, *Oncorhynchus mykiss* (Narum *et al*., 2013a) in warmer environments. However, genome scans alone only identify genes of large effect. Identifying such genes is often not representative of the subtler changes in allele frequencies associated with local adaptation and also requires *a priori* knowledge of the selection pressure to imply any causation (Rellstab *et al*., 2015). Landscape and seascape genomics are emerging fields, derived from landscape (Manel *et al*., 2003) and seascape genetics (Galindo *et al*., 2006), that seek to address this by directly correlating allele frequencies with environmental variables that may be important drivers of patterns of local adaptation. For example, allele frequencies of the β-galactosidase gene, which is known to play an important role in cold tolerance, in populations of American lobster, *Homarus americanus,* along the Atlantic coast of North America, were correlated with sea surface temperature (Benestan *et al*., 2016). The fields of landscape and seascape genomics are still in their infancy compared to independent genome scans but hold great promise in identifying which landscape variables influence the structuring of genetic variation (Meirmans, 2015; Riginos *et al* 2016). Moreover, they are only likely to become more frequently utilised not only due to NGS making greater numbers of markers available but also with great improvements in environmental datasets and their accessibility (Riginos *et al*., 2016).

Towards a better Understanding of Plasticity and Adaptation

Ecological and genomic approaches both increase our understanding of adaptation and plasticity but from different perspectives. Genomic approaches seek to investigate the underlying process while ecological approaches seek to describe higher level patterns. In order to develop a holistic understanding of plasticity and adaptation, from the level of the genes through to population-level responses, the two approaches must be effectively combined. To achieve this, phenotypically rich data gathered from ecological studies and genotypically rich data from NGS genome scans should be integrated into an emerging field of quantitative genetics, which links genotype and phenotype in a meaningful way (Figure 4).

In model organisms, this link could be made by crossing inbred pedigree lines of known genotype and phenotype. By scoring the phenotypes of F_1 and F_2 generations and associating this to genetic variation it is possible to identify Quantitative Trait Loci (QTL) responsible for phenotypic traits (Shrimpton and Robertson 1988; Mackay 1995, Erickson *et al*., 2004). However, pedigree crossing is a timely process and many species do not lend themselves to being bred over multiple generations in a laboratory environment (but see Everett and Seeb, 2014). Moreover, such studies do not reveal how traits respond to selection in the wild. More recently, the high density of markers provided by NGS has allowed Genome Wide Association studies (GWAS) to be performed in wild populations (i.e. no pedigree information), of ecologically-important taxa. GWAS are similar to pedigree crosses in that they statistically associate genetic variation to scored phenotypic traits (Hayes and Goddard, 2010) and allow the polygenic basis underlying phenotype to be determined by analysing the joint effects of different allele frequency combinations (Berg and Coop, 2014). GWAS therefore provide an effective method to link phenotype to genotypic variation in 'wild populations' without the lengthy and iterative process of pedigree crosses (Stinchcombe and Hoekstra, 2008; Slate *et al*., 2010). For example, GWAs in wild populations of salmon, *Salmo salar,* have been used to effectively identify areas of the genome responsible for age of maturation (Barson *et al*., 2015) and age at which they return to freshwater to spawn (Johnston *et al*., 2014). However, wild GWA studies are still subject to the confounding effects of phenotypic plasticity, as determining whether the phenotype being scored is due to plasticity or adaption remains challenging. This leads to issues with identifying thermal phenotypes (along a latitudinal gradient for instance) and may be a reason why, to date, no study has linked thermal phenotype to genotype in this way (Porcelli *et al*., 2015).

Plastic traits can be disentangled from adaptation using common garden and transplant studies (Table 1). Therefore, there is real scope to not only use ecological genomics and

common garden/transplant experiments to yield insights into adaptation, but to directly link phenotypic traits with the underlying genomic variation (de Villemereuil *et al.,* 2016). By using the phenotypically rich data provided by ecological methods (e.g. thermal tolerance) and the large number of markers provided by genome scans it is possible to conduct effective GWA studies without the confounding effects of plasticity seen in wild populations (de Villemereuil *et al.,* 2016). A single experiment would yield not only two lines of evidence (phenotypic and genotypic) to infer adaptation but allow both genotype and phenotype to be effectively linked together (Figure 4), which has been rarely achieved outside of model systems.

Common garden experiments and genome scans can also be combined to investigate the epigenome, the basis of transgenerational plasticity. By using methylation sensitive enzymes the methylation state of the genome can be assessed. If this is conducted before and after a stimulus to a parental generation and methylation state of the genome is tracked in subsequent generations, it is possible to determine cause and effect relationships between loci methylation and change in phenotype. Schield *et al*., (2016) successfully used this 'EpiRADseq' approach to identify shifts in the epigenome of the water flea, *Daphnia ambigua*, in response to fish predator cues. In the context of thermal physiology, transgenerational plasticity is particularly relevant for heatwaves. If a parental generation is subjected to a heatwave, epigenetic changes may make this population more resilient to future similar events. This increased resilience could then be inherited by subsequent generations (Salinas and Munch, 2012). Thus, such heritable plasticity could be a mechanism by which populations can rapidly acclimate to future warming. Seagrasses therefore present themselves as an ideal model group to test this owing to their asexual growth strategy and the current research interest surrounding their vulnerability to heatwaves. Asexual clonal shoots are genetically identical and so by using them in experimental and control groups any confounding effects that genotypic variation may have on interpretations are negated.

As the potential for NGS is realised, novel integrations and approaches utilising this technology will also become apparent. For example, there has been recent discussion regarding using transcriptome profiling to measure thermal safety margins *in situ* (Evans and Hofman, 2012). While Hsp upregulation can be used to quantify thermal stress it is often reversible. Once temperatures cause irreversible damage to proteins, genes related to proteolysis and cell cycle regulation will be up upregulated (Kultz, 2003, 2005; Hofmann, 2005). The identification of such transcripts may be used by managers to predict when

populations are at their upper tolerance limits and has recently been suggested as a strategy to predict bleaching events in corals (Evans and Hofmann, 2012). By using such an approach in populations during peak summer temperatures or during specific heatwave events it may be possible to determine how close populations are to their thermal limit, *in situ*, before major differences in physiology are apparent and population-level responses ensue.

Conclusions

We have shown that intraspecific variation in thermal niche is widespread in marine macrophytes. In order to directly assess what this means for central population vulnerability, targeted studies are required that effectively link these differences against future warming scenarios. Insight in this regard is being gained in terrestrial forests where large historic provenance datasets are facilitating the calibration of Environmental Niche Models (ENMs) (e.g. Aitken *et* al., 2008; O'Neil *et al.,* 2008; Valladeras *et al*, 2014). However, similar advances in other systems are impeded by a lack of fine scale data. Therefore, a first step should be to test concepts across systems and collect relevant empirical data to allow for extrapolation from local to regional and global scales. In this way generalisations may be made that can be applied across phylogenies. It should also be stressed that this will still only be a first step in accurately assessing species responses as accurate predictions may also be further clouded by potential interacting effects of other anthropogenic factors (Crain *et al*., 2008). For example, the greater availability of CO_2^- ions from ocean acidification may, to some degree, ameliorate negative effects of warming (Koch *et al*., 2013) and may give macrophytes a competitive edge over other species (Diaz-Pulido *et al*., 2011).

We have also shown that NGS platforms have not yet been utilised in the study of marine macrophytes and, as a result, a mechanistic understanding of plasticity and adaptation remains elusive in these systems despite recent advances in coastal fauna. Given the literature indicates that variability in thermal physiology is seemingly commonplace in this group, and considering that forest-forming marine macrophytes are of considerable ecological and socioeconomic importance, they present themselves as excellent candidates to determine the molecular basis for thermal plasticity and adaptation. We also highlight that ecological and genomic techniques are often complementary to one another and by integrating these fields resources can be maximised and maximum insight gained. Such interdisciplinary experiments will elucidate patterns and processes across all levels of

biological organisation which will result in a more complete and holistic understanding of adaption and plasticity, bridging the gap between macroecology and ecological genomics.

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FIGURE LEGENDS

FIGURE 1: Predicted responses of low and high dispersing species to increases in temperature, at both the trailing edge and range-centre of their biogeographic distributions. Each oval represents a changing thermal niche at the trailing edge or range centre as warming progresses. Low dispersing sessile species (e.g. marine macrophytes, pictured) that exhibit intraspecific differentiation in thermal niche will not be able to disperse into future suitable niches and will become locally extirpated as warming progresses. This could see local extinctions at species trailing edge and range centre. In high dispersal or highly mobile species (e.g. fish, pictured) local extinctions at species trailing edges will occur but warm-tolerant climate migrants should be able to track suitable extant habitat by migrating or dispersing to different parts of their range resulting in species persistence at the range centre.

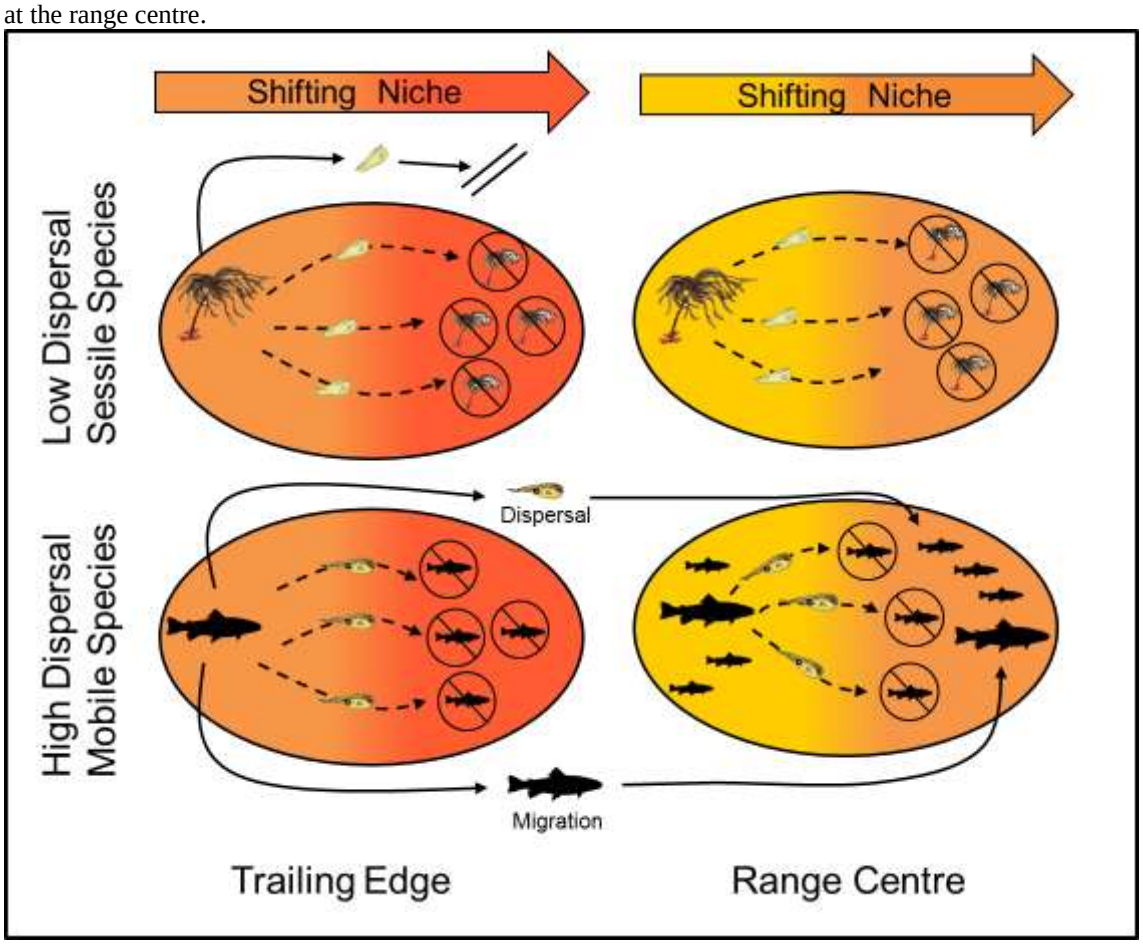

FIGURE 2: Distribution of sampling sites of 42 studies (identified in this review) investigating differences in thermal phenotype of geographically separated macrophyte populations. Numbers in main map refer to specific geographic areas shown in greater detail below. Each data point represents an individual sampling site. Different colour data points indicate different taxonomic families. * Indicates images from authors. + Indicates images from Frances Bunker.

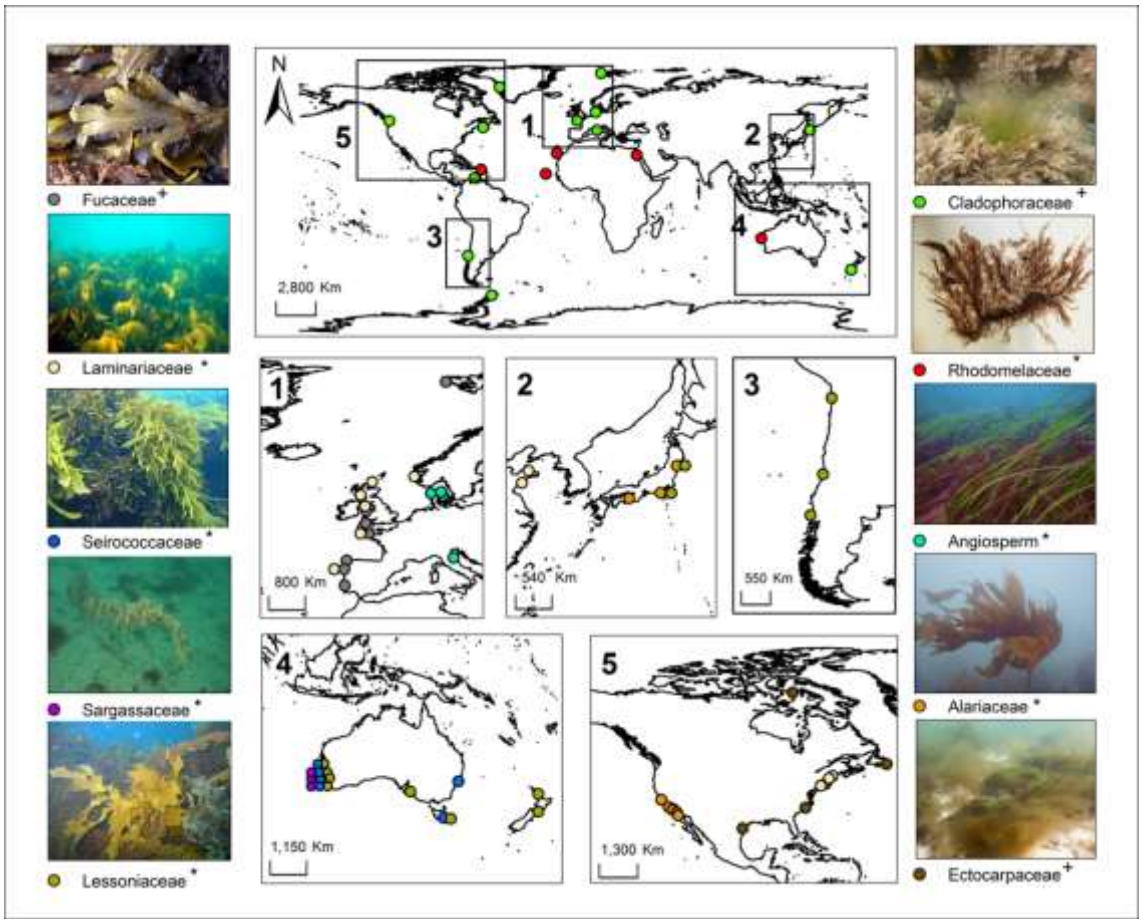

FIGURE 3: Characteristics of experimental studies of intraspecific variation in thermal physiology of geographically separated macrophyte populations (n = 42 papers). CG = common garden experiment 171x121mm (300 x 300 DPI).

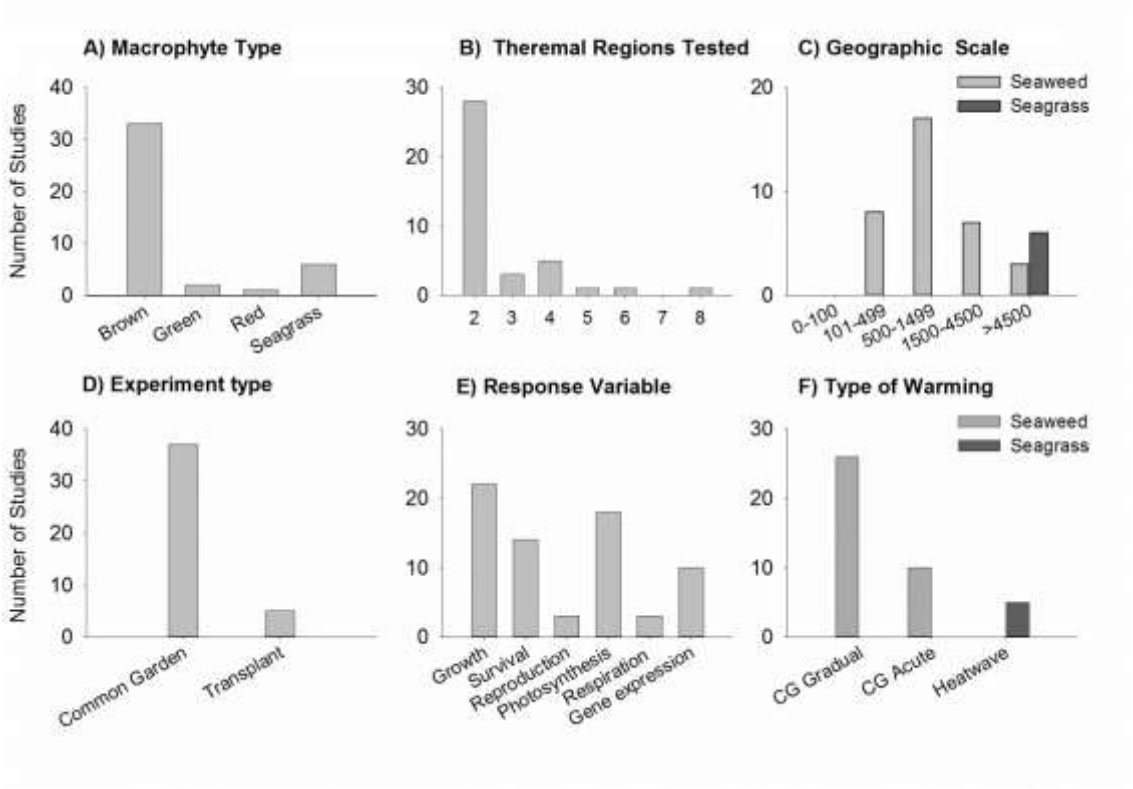

FIGURE 4: A) Current approach to measuring plasticity and adaptation. B) Potential for combination of ecological genomics and macroecology. C) Definitions of mechanistic understanding that can be gained using molecular tools and ecological techniques with examples or potential future uses. Coloured lines between ecological techniques and molecular tools indicates where combining approaches can lead to greater understanding. Rec trans = Reciprocal transplant, CGS = Common garden study.

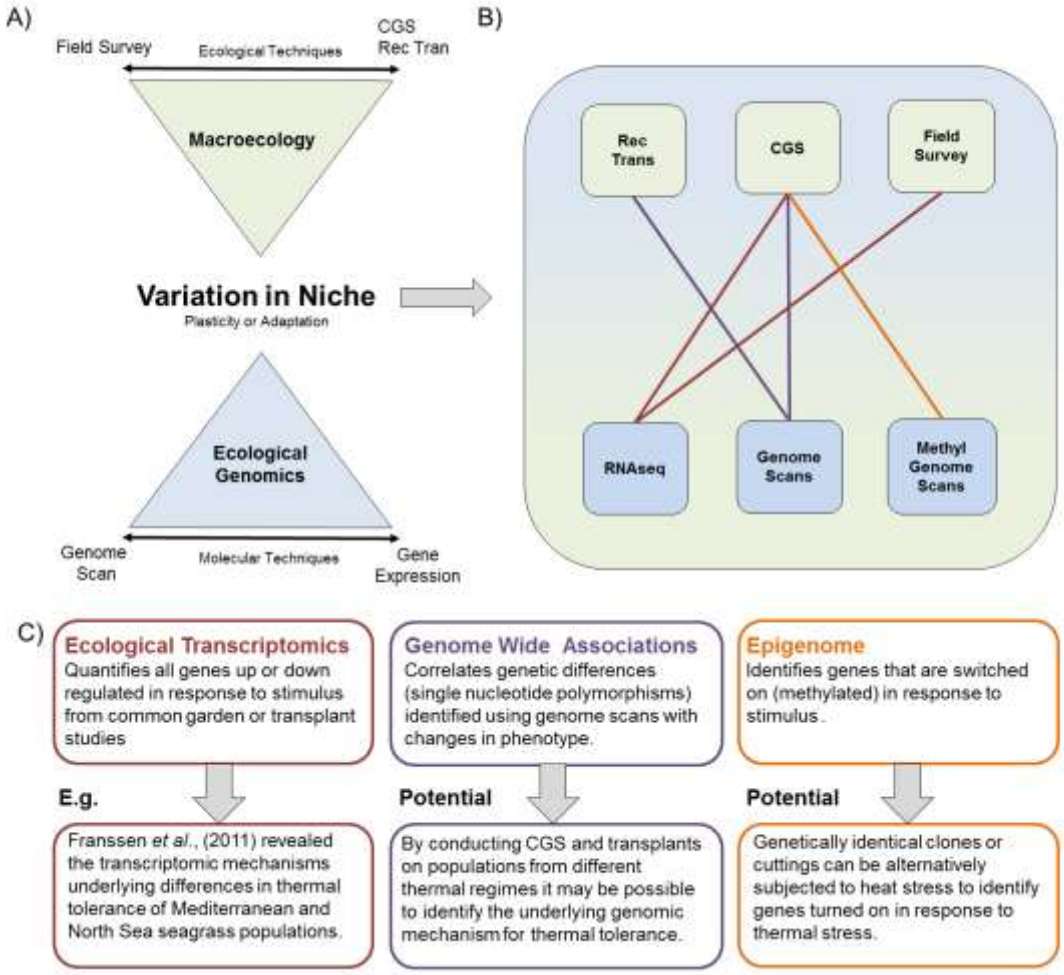

Table 1. Approaches to Measuring Plasticity and Adaptation

Study Type	Summary	Advantage	Disadvantage
Measuring Ecological Pattern			
Common Garden Studies (CGS)	Expose individuals to the same experimental manipulations in a common setting.	• Can identify single variables as drivers for differences. • Comparatively cheap and simple.	• May neglect potential effects from other environmental differences experienced between the tested populations.
Transplant	Relocate individuals or seeds from one population directly to the area of another	• Incorporates all environmental variation between sites.	• Difficult to disentangle co varying environmental factors. • Manpower, cost and logistical challenges. • Concerns regarding genetic contamination
Multi-generation	Rear offspring from different populations over multiple generations. Conduct CGS or transplants on F_2 or F_3 offspring.	• Can eliminate transgenerational plasticity.	• Difficulties rearing marine species through their life cycle in aquaria. Requires long term (years) studies.
Measuring Molecular Mechanism			
Gene Expression			
qPCR	Uses number of PCR cycles to quantify mRNA against control.	• Low cost • Least biased results	• Limited to small number of genes (~30)
cDNA Microarrays	DNA probes printed onto 'chips'. Fluorescently tagged samples are allowed to bind to chip. Intensity of florescence used as proxy for expression.	• Allows many genes to be quantified	• Requires prior knowledge of sequence • Cannot discover new genes
RNAseq	NGS used to sequence the entire transcriptome.	• Transcriptome wide quantification • Identifies transcripts with no prior knowledge of sequence	• High cost • Requires high computing power • Expert bioinformatics required
DNA sequences			
Genome scans	Genotyping large numbers of Single Nucleotide Polymorphisms (SNPs) permits identification of SNP's under selection.	• In some cases outlier loci can be annotated to reveal potential ecological function. • Ecological association tests may permit identification of environmental drivers of selection	• Only identifies genes of large effect and provides little insight into architecture of polygenic adaptation. • May confound multiple types of selection • Difficult to link signatures of selection to specific phenotypes.

Box 1. What are Adaptation and Plasticity?

Adaptation occurs due to changes in allele frequencies, through natural selection, that results in a shift towards a local optimum for respective populations. This can act on pre-existing standing variation within each population or on new mutations (Hermisson and Penning, 2005). Alternatively, the structure of regulatory proteins can change resulting in new patterns of gene expression. This can result in certain genes being 'switched' on or off as well as altering the magnitude of expression, both of which can alter phenotype (McDonald *et al*., 1977; Carroll, 2000).

Phenotypic plasticity is the ability of a single genotype to modify its phenotype in response to changing conditions and can be modulated through changes in gene expression. 'Epigenetic' mechanisms such as histone modification, chromatin remodelling, small interfering RNA's, and DNA methylation can change gene expression profiles, while not altering the underlying DNA sequence (Bossdorf *et al*., 2008; Kelly *et al*., 2012). Not all of these are reset in the next generation and can form the basis of transgenerational plasticity. The mechanisms underlying this non-DNA based inheritance are poorly understood but DNA methylation is emerging as a key route.